

Sound production and cannibalism in larvae of the pine-sawyer beetle *Monochamus sutor* L. (Coleoptera: Cerambycidae)

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One-year old larvae of the pine-sawyer beetle, *Monochamus sutor* L. (Coleoptera: Cerambycidae), produced regular, chirping sounds, easily heard up to 10 meters away. Larvae were positioned within their hibernation tunnel in sapwood of recently fire-killed spruce and pine trees. Their heads were directed outwards, and the sound was probably produced by the scratching of their mandibles against the bark. Since the larvae produce this sound in spite of the risk of attracting parasites and predators such as wood-peckers, this behaviour most likely has an adaptive value. We suggest that sound production helps a larva to secure resources around its hibernation tunnel for its own development by keeping away other potentially competitive larvae. That the larvae are cannibalistic was demonstrated during a trial performed in petri dishes filled with sawdust. Any larva ignoring the sound signal could therefore face a real threat of being killed.

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Strange chirps in burned forests

During visits in some forest areas burned over the past year in Central Sweden (Fig. 1), a regular, chirping sound could be heard from fire-killed spruce (*Picea abies*) and pine (*Pinus silvestris*) trees. The sound was heard during sunny weather at the end of June 1995, and consisted of three to four chirps (sounding like a finger-nail being scratched repeatedly over a comb), together lasting for about 2 sec. The sound was repeated at intervals of five to ten seconds or longer. Several sources of the sound were heard in different trees simultaneously, and the sound could be detected at a distance of more than 10 meters. By exactly locating the sound and removing the bark, larvae of the pine-sawyer beetle, *Monochamus sutor* L. (Coleoptera: Cerambycidae), were invariably found. These were most likely one year old, as colonisation by pine-sawyer beetles take place immediately after fires, at least when fires occur during July and August (Forsslund 1934 and personal observations). The larvae were positioned in the sapwood, each inside its hibernation tunnel, with

their heads projecting outwards against the bark (Fig. 2). They presumably produced the sound by scratching their mandibles against the bark. As the sub-cortical tissue of a tree is more or less consumed after attack the space beneath the bark is air-filled and can act as a resonance chamber. No feeding was observed in connection with sound production. Hence we can exclude the possibility that it is a by-product of feeding.

In central and northern Sweden, the pine-sawyer beetle has a two year life-cycle. During the first summer of development, larvae live entirely sub-cortically whereas in their second summer larvae make a hibernation tunnel into the sapwood (Fig. 2). However, extensive feeding excursions are still made under bark adjacent to the hibernation tunnel. After passing a second winter, larvae pupate early in the following summer. The pupa is formed at the innermost end of the now U-shaped, 5-10 cm deep and 20-25 cm long tunnel. Emergence of adult beetles take place in July to August the same year, the third summer of development.



Fig. 1. Burned pine forest 15 months after a fire. Pines showing signs of foraging by black woodpeckers *Dryocopus martius* and three-toed woodpeckers *Picoides tridactylus*. The woodpeckers have been searching for larvae of the pine-sawyer beetle *Monochamus sutor* and other beetles. Brattforscheden, Värmland, south-central Sweden, October 1993. Photo: Sven-Åke Berglind.

Bränd tallskog 15 månader efter brand. Tallar med spår efter födosök av spillkråka och tretåig hackspett. Hackspettarna har sökt efter larver av tallbocken och andra skalbaggar. Brattfors brandfält, Värmland, oktober 1993.

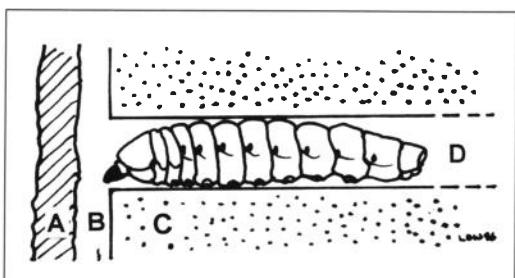


Fig. 2. Larva of the pine-sawyer beetle *Monochamus sutor* in the same position as when sound is made. A) bark, B) air-filled space, C) wood, D) hibernation tunnel.

Larv av tallbocken i samma läge som när ljudalstringen sker. A) bark, B) luftfyllt mellanrum, C) ved, D) övervintringsgång.

What is known about larval sound production in beetles

Sound production in beetle larvae, excluding that produced by feeding, is very rare (Crowson 1981). The first known example is of the gregariously living chrysomelid beetle *Paropis* sp., whose larvae produce sound by tapping their abdomens against the leaves of *Eucalyptus* on which they live (Meyer-Rochow 1972, cited in Crowson 1981). The behaviour is assumed to synchronise a defensive reaction against predators.

In Japan, Izumi et al. (1990) reported larval sounds in the close relative *Monochamus alternatus* Hope and gave a detailed description of the sound. They were similar in strength to those we heard (audible up to 15 meter away), and were recorded as having a sound pressure of 40 dB. The

sound of this species consisted of sound-units, or chirps, that had a length of 0.04 seconds and were repeated with an intersound interval of 2 seconds. They established that the sound was produced by the scratching of mandibles against the beetles gallery walls, but gave no explanation why larvae produced sound.

Leiler (1992) described the sounds of two other cerambycid larvae, *Niphona pecticornis* Muls. and *Ceroplesia aetuans* Ol. These bored inside wood and presumably made their sound by knocking their heavily sclerotised mandibles downward against the wall of the air-filled larval burrows. Both these species belong to the subfamily Lamiinae, as does *Monochamus*. Leiler (1992) suggested that the vertical type of head of lamiinae larvae could be especially well suited for sound production. He speculated that the function of the sound would be to synchronise hatching. However, in *Monochamus* this is not very probable as hatching does not occur until a year after sound production.

Izumi et al. (1990) found that sound production by individuals decreases during *M. alternatus* larval development. During later larval stages, when the sub-cortical tissue has been consumed, larvae live progressively more inside the wood than under bark.

If sound is produced and has some functional significance, it ought to be perceived. Many wood-living beetle larvae (e.g. Buprestidae and Cerambycidae) have chordotonal organs attached to the pleural discs in the abdomen (Saliba 1972). The hearing function of these organs has been revealed through dissections and comparative anatomical studies in *Monochamus confusor* Kirby, a North-American species closely related to *M. sutor* (Hess 1917). Thus sound production in *M. sutor* may serve some intraspecific function.

Monochamus larvae can be cannibalistic

To test if larvae of *Monochamus sutor* were cannibalistic, a trial was conducted in which two larvae were placed in wetted sawdust in petri dishes (57 mm diameter). Larvae were collected from a burned forest stand at Prästvallen in the province of Dalarna (61°22' N, 14°35' E, 520 m a.s.l.) at the end of June. They were found under the bark of burned spruce trees at between a half

Tab. 1. Results of predation experiment with pairs of pine-sawyer larvae *Monochamus sutor* in petri dishes with sawdust. The weight of larvae at the start of the experiment and the outcome are presented (* cannibalised larvae).

Resultat av predationsexperiment med par av tallbockslarver i petriskålar med sågspån. Larvernas vikt vid försökets början samt utfallet presenteras (* äten larv).

Weight of larger larvae (g)	Weight of smaller larvae (g)	Outcome of interaction
0.0905	0.0295*	cannibalism
0.0699	0.0444*	cannibalism
0.3414	0.0420*	cannibalism
0.0750	0.0334*	cannibalism
0.0772	0.0114*	cannibalism
0.0726	0.0365	no cannibalism
0.1242	0.0451	no cannibalism
0.0951	0.0426	no cannibalism

and two meters above ground. The lower limit of their distribution on trees normally coincided with burrows of the buprestid *Melanophila acuminata* DeGeer, which prefers to burrow into the basal part of trees. Larvae were then kept in plastic jars at 8°C for five days. To prevent dessication, moist, green moss was put in the jars. The larvae remained active and mobile until the onset of the trial. They ranged in weight between 0.011 and 0.341 g with an average of 0.118 g (Tab. 1). The difference in weight between the two larvae in trials ranged between 0.025 and 0.299 g. The large variation in weight could be due to the fact that the time for larval development is variable in this species (Forsslund 1934). To prevent larvae from escaping, a plastic lid with holes for ventilation was fitted on each dish. The larvae were then left to interact for six to eleven days at room temperature and in complete darkness.

In five out of eight petri dishes, the larger larva predated the smaller (Tab. 1). Remains of larvae, such as mandibles or whole head-capsules found in the sawdust, was taken as evidence of predation.

Unfortunately the larvae were not determined to species before the experiment. After the experiment it was possible to determine 12 out of 16 specimens to species, all of which were *M. sutor*. Gi-

ven the habitat and position on the trees where the larvae were found, we think it is a safe assumption that the other four larvae were also *M. sutor*.

Hellrigl (1971) also noted that *M. sutor* has a cannibalistic tendency. By examining logs for eggs, larval burrows and adult exit-holes, Rose (1957) estimated that cannibalism was the largest mortality factor in *M. scutellatus*, a North-American species with very similar biology to that of *M. sutor*; both among first-, second- and third-instar larvae of *M. scutellatus*, cannibalism was the main mortality factor (together more than 80 % were killed). Woodpeckers caused 12 % mortality, mainly in the third and fourth larval instars (when the larvae had bored into the wood). Mortality caused by desiccation and parasites as well as by invertebrate parasitoids and predators was considered less important.

Why sound production?

For a beetle larva living under bark, it seems hazardous to emit any sound. That hymenopteran parasitoids use sound to find their host is doubtful (Vinson 1976, Alphen & Vet 1986), even if vibrations through the substrate probably can guide them (Matthews & Matthews 1978). However, it is likely that sounds can guide other enemies, like woodpeckers and other insect parasitoids, to the larva. Therefore this recorded sound production must have some other, strong, adaptive value.

Forsslund (1934) showed that *M. sutor* needs sub-cortical tissue to complete its development. Sapwood is not enough. As the sub-cortical tissue normally becomes totally consumed by *Monochamus* larvae one year after attack (Trägårdh 1929, Rose 1957), increasingly severe competition for the remaining resource arises. We observed that *M. sutor* larval burrows under bark become very long (30-50 cm), which suggests that one year old larvae have to move considerable distances to find enough food.

Perhaps sound production by *Monochamus* larvae is some kind of territory defence mechanism. Thereby a sound producing larva could secure resources for itself and increase the possibility of acquiring enough energy for pupation. Since we showed in the petri dish experiment that large larvae can indeed cannibalise smaller ones, sound production would be a case of honest signalling. A

larva that ignores the territorial behaviour of a signalling larva faces a potential danger of being seriously injured or killed.

Sound can be used as a cue for larvae to avoid a certain part of the tree-trunk. Hellrigl (1971) speculated that larvae of *M. sutor* could locate their conspecifics by their chewing sounds produced during feeding, and thereby avoid being cannibalised. Saliba (1972) showed in laboratory experiments that cerambycid larvae of several species were able to avoid each other by moving away from chewing sounds. Larvae approaching each other turned away at sharp angles well before meeting, and this behaviour could be manipulated by mimicking the sounds artificially.

It is probably safer for *M. sutor* larvae to produce sound while in a hibernation tunnel rather than under bark. In the tunnel, they can quickly move backwards and protect the tunnel entrance with their sclerotised head and well-developed mandibles. This is probably a sufficient defence against other larvae, though probably not against woodpeckers.

Whether sound production definitely functions as a territorial defence signal remains to be shown experimentally. A possible next step would be to mimic the sound and observe behavioural responses directly. Another approach would be to see if sound production differs between small and large larvae as well as to see how the density of larvae and amount of resources under bark affects this behaviour.

Acknowledgement

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Sammanfattning

Vid besök på två brandfält i slutet av juni 1995 vid Särna och Orsa i norra Dalarna (brända i juli 1994) hördes regelbundna skrapläten från branddödade granar och tallar. Det låt ungefärligt som när man drar fingernageln flera gånger över en kam, 3-4 ljudstötter som tillsammans varade ca 2 sek upprepades med 5-10 sek intervall, ibland längre. Flera ljud kunde höras samtidigt och de var klart urskiljbara på över 10 meters håll i lugnt väder. Genom att exakt lokalisera ljudkällan med hörseln och snabbt riva av barken hittades larver av tallbock *Monochamus sutor* L. (Coleoptera: Cerambycidae). De satt med huvudet riktat utåt i sin övervintringsgång inuti veden (Fig. 2). Ljudet frambringas förmodligen genom att larverna skrapar käkarna mot barken. Inga direkta gnag kunde observeras i samband med ljudalstringen, varför vi anser oss kunna utesluta att ljuden är en biprodukt av detta. Då ljudalstringen potentiellt kan locka till sig fiender utifrån, som hackspettar och parasitoida insekter, bör beteendet ha fördelar som starkt väger upp detta. Vi föreslår att ljudalstringen hjälper larven att hålla andra larver borta från resurserna runt dess övervintringsgång. Mot slutet av larvutvecklingen råder konkurrens om kvarvarande kambium under bark. Ett beteende som ökar en individs chans att monopolisera tillräckliga resurser inför förpuppningen bör ha ett högt adaptivt värde. I ett försök med 1-åriga larver i sågspän visade det sig att de är starkt kannibalistiska. Så lunda kan andra larver som ignoreras signalen löpa en högst verlig risk att bli dödade om de kommer för nära.

Rättelser och förklaringar till Sveriges myror

Redaktören har med berömvärd ihärdighet övertygat mig att närmare förklara hur en myra kan ha ett halvt borst, vilket påstås i punkt 16 i bestämningstabellen för *Formica* på sidan 96 i min artikel *Sveriges myror* i ET nr 3 1995. Det skulle naturligtvis ha stått "I snitt färre än 0,5 utstående borst ..." respektive "I snitt minst 0,5 utstående borst ..." När man bestämmer myror är det en stor fördel att ha tillgång till flera individer från samma samhälle och för vissa *Formica* och *Lasius* är det alldelvis nödvändigt om man ska känna sig nå-

gorlunda säker på artbestämningen. Gången vid bestämningsarbetet är således att man räknar antalet borst på låt säga fem individer (givetvis från samma bo/samhälle), räknar ut medelvärdet och använder detta när man nycklar i tabellerna.

Redaktören har också påpekat fel i tabellen på sidan 96. Punkt 11 första alternativet ska föra vidare till punkt 12 (ej 13 som det står) och punkt 12 andra alternativet ska hänvisa till 13 (ej 12).

Per Douwes